

PHITYCOLAX, A NEW GENUS OF ADELPHOPARASITIC RED ALGAE FROM ILE AMSTERDAM, SOUTHERN INDIAN OCEAN

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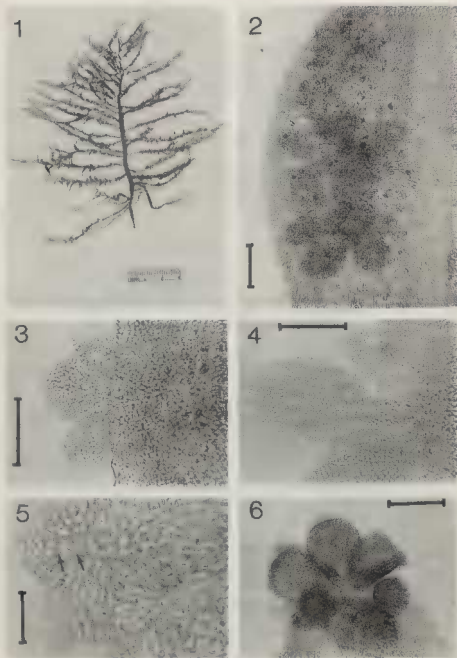
ABSTRACT - *Phitycolax inconspicua* gen. et sp. nov. is a hemiparasitic red alga occurring on *Phytomphora amansioides* (Sonder) Womersley collected at Ile Amsterdam (Fr.) in the southern Indian Ocean. Both taxa are assigned to the *Hypoglossum* group of the Delesseriaceae (Ceramiales). *Phitycolax* is the only parasite in the subfamily Delesseriaceae, in contrast to the sub-family Nitophylloideae, which contains four parasitic genera. Thalli consist of small (up to 2mm across) tufts of narrow blades reaching to 1.0mm length. Spermatangial, carpogonial cystocarpic, and tetrasporangial thalli are described, and criteria for distinguishing true parasites hemiparasites from vegetative outgrowths or syntagmatic tetrasporangial germinations on the host are considered and discussed.

RÉSUMÉ - *Phitycolax inconspicua* gen. et sp. nov. est une algue rouge hémiparasite qui se rencontre sur *Phytomphora amansioides* (Sonder) Womersley récolté à l'Ile Amsterdam (Fr.) au sud de l'Océan Indien. Ces deux taxons sont rapportés au groupe *Hypoglossum* des Delesseriaceae (Ceramiales). *Phitycolax* est le seul parasite connu dans la sous-famille des Delesseriaceae, alors que la sous-famille des Nitophylloideae contient quatre genres parasites. Les thalles forment de petites (jusqu'à 2mm) touffes de lames atteignant 1mm de longueur. Les gamétophytes mâles, femelles (avec cystocarpes) et les tétrasporophytes sont décrits; les critères pour la distinction entre les vrais parasites hémiparasites et les excroissances végétatives ou les germinations tétrasporangiales syntagmatiques sur l'hôte sont examinés et discutés. (traduit par la rédaction).

KEY WORDS : adelphoparasite, Delesseriaceae, Ile Amsterdam, marine algae, parasitic red algae, *Phitycolax inconspicua* gen. et sp. nov., Rhodophyta, southern Indian Ocean.

INTRODUCTION

Four genera of parasitic Delesseriaceae are presently recognized, all adelphoparasites assigned to the sub-family Nitophylloideae: *Asterocolax* (Feldmann & Feldmann, 1951), *Gonimocolax* (Kyllin, 1924), *Gonimophyllum* (Batters, 1892),



and *Polycoryne* (Skottsberg in Kylin & Skottsberg, 1919). A tetrasporangial specimen of *Phytomophora amansioides* (Sonder) Womersley, collected at Ile Amsterdam, bore numerous tufts of minute, lightly pigmented blades. Separate male and female gametophytes, as well as tetrasporangial thalli, were present and, like the host, had an apical organization conforming to the *Hypoglossum* group. The discovery of these growths raised the question of whether they represented a genuine independent genus or were merely precociously fertile germings developing *in situ* on the parent plant.

Ile Amsterdam (also known as Nouvelle-Amsterdam and Neu Amsterdam) lies at 37°50'S, 77°32'E in the southern Indian Ocean, forming part of the "Parc national antarctique français" (Clark & Dingwall, 1985). The island is just north of the Sub-tropical Convergence (Delépine, 1966) and has a warm-temperate marine flora with sea surface temperatures of 10-15°C in winter and 15-20°C in summer (Knox, 1960). The algal flora lacks *Durvillaea* but does have *Macrocystis pyrifera* (L.) C. Ag., *Laminaria pallida* (Grev.) J. Ag., and *Splachnidium pygmaeum* (L.) Grev., causing Delépine (1963) to point out a biogeographic connection linking Ile Amsterdam to Tristan da Cunha and South Africa. Older references to the marine algae of Ile Amsterdam and nearby St. Paul Island include those by Grunow (1869), Reichardt (1871), and Reinhold (1907, 1908).

MATERIALS AND METHODS

The host was collected in drift 20 meters offshore from the NE (leeward) face of the island, 2kms from the meteorological station, on 2 April, 1987, by the second author. A cystocarpic specimen of *Phytomophora* without the parasite was also found amid specimens collected by F.J. Scott and Dorle Pauli, 5m offshore in the same area, on 1 April, 1987. Both collections were pressed as herbarium specimens. Small pieces of dried host tissue, on which the parasite could be seen with a dissecting microscope, were removed and mounted on slides for microscopic observation. Permanent slides were prepared by ringing the cover slip with 40% liquid glucose (Karo syrup). Photographs were taken on a Zeiss research microscope. The slides with the parasite have been deposited in MICH (Univ. of Michigan Herbarium, Ann Arbor), PC (Cryptogamic Division of the Museum national d'Histoire naturelle, Paris), MELU (Univ. of Melbourne Herbarium, Parkville), and UC (Univ. of California Herbarium, Berkeley).

Fig. 1-6 - Fig.1. *Phytomophora amansioides*. Fig. 2-6. *Phitycolax inconspicua*. Fig.1. Host specimen. Figs 2, 3. Spermatangial thalli. Fig. 4. Blade with spermatangial sorus. Fig. 5. Blade bearing carpogonial branches (arrows) on primary cell row. Fig. 6. Cystocarpic thallus (= Holotype). Scale bars: 3cm in Fig. 1; 100µm in Fig. 2-4; 30µm in Fig. 5; 200µm in Fig. 6.

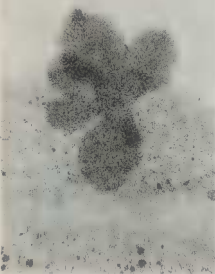
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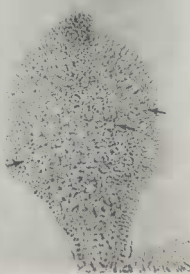
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DESCRIPTION

General morphology

Clusters of the outgrowths are randomly distributed across the blades of the host (Figs. 2 and 9). This distribution of proliferations is not normally encountered in the host (Fig. 1), where branching is restricted to the midrib. Each outgrowth usually consists of a cluster of 5 or 6 simple blades, but may be a single blade or as many as twelve. An entire cluster measures 500-750 μm across (for male thalli) (Fig. 2), 630-1200 μm across (for female cystocarpic thalli) (Fig. 6 and 7), 700-2000 μm across (for tetrasporic thalli) (Fig. 8). A cluster is attached by a common base which extends rhizoids into the host tissue.

Apical organization of the outgrowths is characteristic of the *Hypoglossum* group, in which all initials of third-order cell rows reach the margin. Not all cells of second-order cell rows bear third-order rows, a condition identical to that of the host (Kuehne, 1946; Wagner, 1954; Wynne, in press). The cutting off of superficial cortication by cells of the primary layer commences close to the apex, resulting in a polystromatic condition, also similar to the host.

The growths appeared to have normal to somewhat reduced pigmentation compared to the host plant, although male thalli appeared colourless. Tetrasporangia are colourless but have highly refractive contents. The growths are attached to the host blade by means of basal filaments that penetrate the tissue of the host. These invasive filaments have small apical cells and consist of uniseriate, multicellular rhizoids that are in contact with host cells by means of secondary pit connections (Fig. 11, arrows). The penetrating filaments are branched and course through the medulla of the host often at some distance from the emergence of the outgrowth. By their narrow rhizoidal nature and their random orientation they can be distinguished from the host cells.

Male gametophytes

Male thalli consist of tufts of simple flattened blades (Fig. 2 and 3). Individual blades measure approximately 250-380 μm in length and 180-220 μm in width. A single continuous spermatangial sorus covers each surface except for the sterile margins (Fig. 4).

Female gametophytes

Carpogonial branches are restricted to the primary axial row (Fig. 5), conforming to the pattern in the sub-family Delesserioideae (Kylin, 1956; Wynne, 1983). Each procarp consists of a single four-celled carpogonial branch and two sterile-cell groups. Fully formed carpogonial branches are present on the 4th segment from the apical cell. Some female tufts bear cystocarps (Fig. 6 and 7), the blades being swollen in the mid or distal region and producing a single cysto-

Fig. 7-10. *Phitycolax inconspicua*. Fig. 7. Cystocarpic thallus. Fig. 8, 9. Tetrasporangial thalli. Fig. 10. Sorus with non-pigmented tetrasporangia (arrows). Scale bars: 100 μm in Fig. 7-9; 50 μm in Fig. 10.

carp. Carposporangia are single and terminal, colourless, and tear-drop shaped, measuring 16-20 μm in length.

Tetrasporophytes

Individual blades of tetrasporic clusters (Fig. 8 and 9) are 350-1000 μm in length and 300-400 μm in width. Tetrasporangial sori are continuous over both blade surfaces, leaving sterile margins (Fig. 10). Tetrasporangia are not covered by cortical cells. The sporangia are spherical irregularly cruciately divided, and range from 8 to 14 μm in diameter. They lack pigmentation, in contrast to the deeply pigmented tetrasporangia of the host, and have highly refractive contents. The tetrasporangia of the host are larger (30-40 μm diameter) than those of the outgrowths.

Diagnosis

Phitycolax Wynne & Scott gen. nov.

Genus adelphoparasiticum Delesseriacearum, conforme Hypoglosso; thallus, e fasciculo minuto lamellarum polystromaticarum, simplicium complanatarumque quae ex adhaesione basali paxilliformi exorient, compositus; rhizoidei in contextum hospitis penetrantes; incrementum per cellulam unicam apicalem et per initia tertiaria quae ad lamellae marginem attingunt; pigmentum normale ad reductum.

Adelphoparasitic genus of the Delesseriaceae, conforming to the *Hypoglossum* group; thallus consisting of a minute cluster of polystromatic, non-proliferous, flat blades from a peg-like basal attachment, with rhizoids penetrating host tissue; growth by means of single apical cell; all tertiary initials reaching the blade margin; blades with normal to reduced pigmentation.

Type species: *Phitycolax inconspicua* sp. nov.

P. inconspicua Wynne & Scott sp. nov.

Parasitica in lamellis Phytomorphorae; thallus fasciculus parvus, fasciculus totus minor quam 2.0mm latitudine; carposporangia elongata, 16-20 μm longa, incolorata; tetrasporangia 8-14 μm diametro, incolorata.

Holotypus: F. Scott 219 in MICH depositus (isotypi in MELU, MICH, PC, et UC).

Parasite on blades of *Phytomophora amansoides* thallus a small cluster of blades, entire cluster up to 2.0mm across; carposporangia elongate, 16-20 μm long, non pigmented; tetrasporangia 8-14 μm in diameter, non-pigmented.

Holotype: F. Scott 219, deposited in MICH (isotypes in MELU, MICH, PC, and UC).

DISCUSSION

Eight genera have recently been assigned by Wynne (in press) to the *Hypoglossum* group: *Bartoniella* Kyl., *Branchioglossum* Kyl., *Chauviniella* Papanf., *Duckerella* Wynne, *Hypoglossum* Kütz., *Phytomophora* J. Ag.



Fig. 11 - *Phitycolax inconspicua* within host tissue. Cells of parasite are stippled. Secondary pit connections (arrows) between host and parasite are observable.

Pseudobranchioglossum Bodard, and *Zellera* Martens. The discovery of *Phitycolax* represents not only an addition to this group but also the first description* of a parasite in the sub-family Delesserioideae. Because of the presence of some pigmentation, *Phitycolax* is more appropriately termed a hemiparasite than a holoparasite (Kugrens & West, 1974). A comparison of the genera of parasitic Delesseriaceae is presented in Table I. *Phitycolax* is clearly separable from related genera primarily by the characteristics that place it in the *Hypoglossum* group.

Goff (1982) has reviewed the various criteria by which diminutive growths on red algae are determined to be genuine parasites hemiparasites, as opposed to bacterial galls or other types of host tissue proliferation. Those which are generally agreed on include: a) reduced size; b) reduced pigmentation; c) presence of both gametophytes and sporophytes on the host; and d) formation of secondary

* Martin & Pocock (1953) reported that *Gonimophyllum africanum*, although usually parasitic on species of *Acrosorium*, did occur on other Delesseriaceae, including *Botryocarpa prolifera* Grev., a member of the Delesserioideae. Feldmann & Feldmann (1958), however, indicate that Martin (*in lit.*) had informed them that only the parasite on *Acrosorium* had been studied in detail and that the parasite on *Botryocarpa* had been identified as *Gonimophyllum* only on the basis of external morphology. Feldmann & Feldmann concluded that the parasite on *Botryocarpa* most likely did not belong to *Gonimophyllum* but probably represented a new genus. New collections of this parasite on *Botryocarpa* are needed to show its possible relationships to *Phitycolax*.

Table 1. Genera of parasitic Desmidiaceae

genus	host	taxonomic placement	morphology (tuft of:)	distribution	mode of growth	Refs.
<u>Asterocleles</u>	<u>Erythraea</u> , <u>Hibiscus</u> , <u>Tradescantia</u> , <u>Phycodryx</u> , <u>Polyneura</u>	<u>Phycodryx</u> group	acicular or clavate axes	Northern Hemisphere	apical cell with transverse divisions	Feldmann & Feldmann, 1951, 1958; Wagner, 1954; Wynne, 1970
<u>Contoplex</u>	<u>Onchidium</u> , <u>Myriophyllum</u> , <u>Schizoseris</u>	<u>Myriophyllum</u> group	simple, lanceolate blades	Northern & Southern Hemispheres	marginal initials with oblique divs.	Kyllén, 1924; Feldmann & Feldmann, 1958, 1961; Beardseth, 1961
<u>Convolvulium</u>	<u>Acrostichum</u> , <u>Cryptogramma</u> , <u>Illecebre</u> , <u>Isotriaena</u>	<u>Cryptopleura</u> group	blades, simple or lobed	Northern & Southern Hemispheres	marginal initials with oblique divs.	Hartn. & Pocock, 1953; Wagner, 1954; Feldmann & Feldmann, 1958; Menzies, 1970
<u>Phytocleles</u>	<u>Phytomphora</u>	<u>Phytocleles</u> group	simple blades	Southern Hemisphere	apical cell with transverse divs.	This paper
<u>Polyneura</u>	<u>Myriophyllum</u> , <u>Schizoseris</u>	<u>Myriophyllum</u> group	acicular or clavate axes	Southern Hemisphere	apical cell with oblique divs. (rare transverse divs.)	Zinova, 1963; Ricker, 1967

pit connections between cells of growths and host. The growths in question fit all of these criteria to qualify as parasites.

Some additional observations can be offered as evidence that the minute clusters from Ile Amsterdam are not merely outgrowths of host tissue. First the large host specimen (Fig. 1) bears tetrasporangial sori on its ultimate bladelets, whereas the minute clusters display three different reproductive somatic phases: gametophytic, carposporophytic and tetrasporophytic. If the tufts were merely vegetative outgrowths of the *Phytomphora*, one would not expect to observe sexual stages.

A second reason for regarding the clusters as an independent alga is that the branching pattern in *Phytomphora* is precise - branches always originate from the midrib of a parent blade by an endogenous production of a branch initial from a primary axial cell. Thus, the various orders of branches in *Phytomphora* are strictly confined to the blade midrib (Wagner, 1954). The fact that the outgrowths are randomly distributed on the host blades, and generally remote from the midribs, suggests that these clusters are not physically related to the host tissues. Furthermore, rhizoids extend from the base of the clusters and penetrate the host tissue, establishing secondary pit connections with the host (Fig. 11).

A similar consideration is whether the clusters represent a distinct adelphoparasitic genus or whether they result from *in situ*, i.e., syntagmatic, germination of tetrasporangia. The fact that some of the epiphytic clusters were tetrasporangial serves to minimize the possibility of these clusters being produced by the *in situ* germination of the tetraspores of *Phytomphora*. The striking difference in the color and size of the tetrasporangia of the clusters and the host is also significant. Therefore, the most reasonable interpretation is that the clusters are an independent parasitic alga with three isomorphic phases (male, female and tetraspor-

ic) and that this alga has a close taxonomic relationship with the host on the basis of apical organization.

Parasitism is a widely occurring phenomenon among red algae, amounting to 50 genera, or approximately 15% of this algal class (Goff, 1982). Of these parasitic taxa, 80% are recognized as adelphoparasites (i.e., very closely taxonomically related to their hosts), and the balance are termed alloparasites. Two different theories have been advocated to explain this high proportion of adelphoparasitism in the red algae. One theory, as first proposed by Sturch (1926) and later supported by Fan (1961), suggests that red algal parasites originated from epiphytes that gradually became parasitic by establishing penetrating organs and means of absorbing food from the host tissue. Fan (1961) regarded the presence of secondary pit connections as a critical factor in the evolution of adelphoparasites.

The second theory, as formulated by Setchell (1918) and supported by Feldmann & Feldmann (1958), hypothesized an origin of red algal parasites by a mechanism involving *in situ* germination of tetraspores and the development of dwarf gametophytes with reduced pigmentation on the parents. Setchell cited the example of *Agardhiella subulata* (C. Ag.) Kraft & Wynne (formerly *A. tenera*), in which *in situ* germination of tetrasporelings is of frequent occurrence. Setchell suggested that such a production of a dwarf phase on the parent can be "a parasitic red alga in the making" and that a further reduction would lead to a parasitic alga. Such an explanation seems feasible in the case of *Phitycolax*.

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